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Live or let live: life-history decisions of the breeding female Monteiro's Hornbill *Tockus monteiri*

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Life-history theory maintains that long-lived species such as hornbills (Bucerotiformes) maximize lifetime fecundity by ensuring adult survival, rather than investing in current reproductive output. Unusually, female *Tockus* hornbills are sealed into the nest cavity during breeding, placing a large burden on the male who feeds her and the nestlings for up to 9 weeks. Early departure to help feed young may improve nestling survival, but could reduce female survival if moult is incomplete. We investigated whether departure time of the female Monteiro's Hornbill *Tockus monteiri* is more strongly related to measures of female fitness or juvenile condition. Departure was independent of nestling development and growth, instead depending on female state. At departure, variability in condition between females was smaller than at any other stage, implying a strong stabilizing selection on optimal female departure condition. Similarly, moult showed signs of being completed, and variability in the state of moult between females was lowest at departure. Both predictions were met in favour of the hypothesis that Monteiro's Hornbills would base the timing of their departure from the nest on maximizing their own survival. Thus, as predicted, future reproductive potential takes precedence over current reproductive output in a trade-off decision in this species.

The trade-off between current reproductive output (survival of offspring) and future reproductive potential (survival of adults) is among the most important life-history 'decisions' animals must make (Stearns 1993). Would it be better for parents to exert themselves to ensure survival of their offspring, or should they save themselves for future breeding attempts? Life-history theory maintains that long-lived species, or species that inhabit highly unpredictable environments, can maximize lifetime fecundity by favouring adult survival above juvenile survival (Erikstad *et al*. 1998, Roff 2002). This is because current offspring have a lower fitness value than future reproductive opportunity (Ghalambor & Martin 2001). The hornbills (Bucerotiformes) are a group of relatively large, long-lived species that should exemplify this adult-biased strategy, and especially arid-adapted species such as the Monteiro's Hornbill *Tockus monteiri*, which inhabits the Namib escarpment with high annual variability in rainfall (Mendelsohn *et al*. 2003).

The unusual reproductive biology of *Tockus* hornbills makes them particularly suitable for a study comparing these two contrasting life-history strategies. In this study we aim to establish which proximate factors determine most strongly the timing of the female Monteiro's Hornbill's departure from the nest. Are they female condition and moult completion, i.e. factors that ultimately enhance future reproductive potential, or nestling condition and development, i.e. factors that ultimately favour current reproductive output? In light of the Monteiro's Hornbill's breeding biology (see below), we set a number of predictions to test the two opposing hypotheses (Table 1). We also investigate as an aside the importance of male provisioning to the 'decision' process.

There are two unusual attributes of *Tockus* biology that are of particular interest here. First, the female obligately seals herself into the nest cavity. Secondly, she undergoes a complete and simultaneous moult of all flight feathers at the commencement of laying, 4–11 days after entering the nest. Consequently, the female and nestlings are entirely dependent on the male for their nutritional needs, and ultimately for their survival. Such a degree of mate dependency is unmatched by other birds (Stanback *et al*. 1999) and demands extreme male investment (Stanback *et al*. 2002). He must pass food to the female through a slit

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Table 1. Predictions used to test the hypotheses of factors that determine the timing of female Monteiro's Hornbill departure from the nest, and ultimately life-history strategy.

Hypotheses: ultimate factors and their proximate explanations	
The timing of female's departure from the nest is determined by factors maximizing:	
Current reproductive output, such as measures related to current breeding success: nestling condition and development	*Future reproductive output, such as measures related to adult longevity: female condition and moult completion, and male provisioning*
Predictions – the female departs …	
1. … when nestling condition deteriorates/ mass–size ratio drops	3. … when her own condition reaches a minimum threshold. Due to stabilizing selection, female condition and variability in female condition is lowest at departure
2. … when nestling growth slows down	
4. … once nestlings are developed enough to perform nest sanitation and reach food passed to them	6. … when her feathers show signs of having completed re-grown. Due to stabilizing selection, variability in female feather re-growth is lowest at departure
5. … once nestlings are well enough developed, so that females from deeper nests depart when their nestlings are larger	
7. Females with males that provide food at a lower rate depart sooner	
8. Females with larger clutches leave earlier	

in the sealed-up nest entrance for up to 70 days (Kemp 1995). During the latter part of this period (up to 25 days) he has the added strain of providing food to growing nestlings. This unusual situation places energetic strains on the male, female and nestlings, and makes it important for the female to time her departure from the nest with care. Her decision should be based on the proximate factors most influential on her own lifetime reproductive output, whether they promote investment in current or future reproduction. Either early or late departure, in relation to these factors, will result in reduced fitness. This should result in a process of stabilizing selection (e.g. Ridley 1993), which reduces variability around optimal departure conditions. Consequently, we expect that departure-determining factors should show a marked reduction in variability between individuals prior to departure, and should reach a minimum at departure.

HORNBILL BREEDING BIOLOGY

Upon entering the nest, the female Monteiro's Hornbill is heavier than normal, with fat reserves and swollen reproductive organs (Kemp 1995). After laying and during incubation the female requires little energy other than that needed for feather regrowth and basal metabolism (Klaassen *et al.* 2003). Her mass increases with male provisioning, reaching a maximum when eggs hatch 24–27 days later (Kemp 1995). Thereafter she relies mainly on body reserves to complete the energy-demanding feather re-growth (Brown 1985, Hohman 1993, Klaassen 1995), losing 9–27% of her mass. However, rapid growth of nestlings requires significant energy inputs from the male (Kemp 1995), and he increases his provisioning rate accordingly (C. Boix-Hinzen unpubl. data). But he cannot always cope with such high demands and starvation of nestlings is not uncommon (Kemp 1995, C. Boix-Hinzen unpubl. data). Once females have left the nest they assist males in feeding young (Kemp & Kemp 1972). This reduces demand for provisioned food, increases the rate of food delivery and should improve nestling survival.

The male's inability to cope with food demands could be reflected in both female and nestling condition; she may be forced to leave when the nestlings reach a threshold of poor condition (P1), or once nestling growth slows considerably (P2). Alternatively, she may depart when her own condition reaches some minimum threshold (P3). Owing to stabilizing selection (discussed above) one would expect differences in condition between females to be smallest when they depart.

Although nutritional demands may favour early departure of the female, certain developmental constraints may delay the female. These, again, can be related either to the nestling or to the female.

Nestlings may need to be sufficiently developed for them to be capable of nest sanitation (Kemp 1995) and/or to reach food passed to them through the nest entrance before the female leaves the nest (P4). Thus, one may expect that females from shallower nests, where nestlings are large enough to reach the entrance at a younger age, would leave earlier (P5). Alternatively, the female's departure may be delayed until her own state of moult reaches a threshold of re-growth (P6). Departure prior to sufficient feather re-growth is likely to reduce her mobility, exposing her to elevated predation risk and/or rendering her a poor forager. Again, because females should attain a common threshold of re-growth, variability in re-growth should be lowest at departure.

If, as a result of insufficient male provisioning, food were a limiting factor, we would expect that females with partners with low feeding rates should leave the nest earlier than those with high feeding rates (P7). In addition, because larger clutches require more food, females with larger clutches should leave earlier, because the male will require assistance sooner (P8). Although the loss of male condition as a result of provisioning workload may also be a factor to drive female departure, we were unable to measure this in the field. However, exclusion of this proximate explanation will not alter the ultimate explanation favouring adult or juvenile survival.

METHODS

Research was conducted at Daan Viljoen Game Reserve (DVGR; 22°32′S, 16°58′E) near Windhoek, Namibia, over the 1999/2000 breeding season (December–April). DVGR is characterized by highland savannah thornveld, with taller stands of trees lining the watercourses. Mean annual rainfall is *c.* 350 mm, most of which falls between November and February, although for the study season precipitation was approximately three times the mean. About 130 nestboxes (dimensions: *c.* 25 × 20 × 50 cm; entrance diameter 60 mm) had previously been erected at *c.* 300-m intervals along access roads as part of an ongoing Hornbill study (Stanback *et al.* 1999). The boxes have removable lids, enabling easy access to the contents of the 80 active nests we monitored over the entire breeding season. Logistical difficulties, such as heavy rain and flooding of rivers, made it impossible to visit all nests when intended. Consequently, sample sizes vary between tests and, because of missing data, are much smaller than 80 for individual tests. As part of another experiment, broods of all but seven of these nests were manipulated by moving eggs or nestlings between them. Because this was done at random, and questions of this study are peripheral to brood composition, the risk of data for this study being biased is minimal. Most nests (84%) contained clutches of three or four eggs.

Dates of relevance to this study were those of female entry to and departure from the nest, egg-laying and hatching, and commencement of female moult. Laying and hatching dates were recorded precisely during visits to nests every 4 days over these periods. Entry and departure dates are less precise; visits were made less frequently (every 6–7 days) at these times because increased disturbance is known to cause birds to desert the breeding attempt or to depart prematurely. The date of entry or departure was assumed to be the mid-point of the range or, in cases where the range was an even number of days, as the first of the two middle days. Females with unknown ranges of more than 4 days were removed from analyses. For disturbance reasons, commencement-of-moult dates were also difficult to record accurately. As feather-moult occurs near the commencement of laying (Kemp 1995, C. Boix-Hinzen unpubl. data), moulting dates are assumed to be the same as those for the day on which the first egg is laid.

Female bill dimensions (length, width and height, measured with callipers; ±1 mm), and nestbox depth (±5 mm; $n = 28$) were each recorded once. To measure box depth we rested the tip of a steel ruler on the nest floor and read the depth to the middle of the entrance slit. Female mass (Pesola spring balance; ±1 g) and primary feather length (the distance from the feather tip to the point where the shaft enters the skin; ±1 mm) were measured every 7 days. Females with fewer than four feather-length measurements were excluded from feather re-growth analyses. Female primary-feather length was recorded for the five odd-numbered primaries. Feathers not yet moulted were assigned a length of 0 mm to indicate that they had not yet started re-growing. Time-series plots of feather growth revealed a near-identical pattern of re-growth for different feathers; we selected the longest primary (P9) for use in this study.

Feather and wing lengths prior to moulting were not measured for this season, so could not be used to control for female wing size. We analysed data from the 1995/96 and 1998/99 seasons to investigate correlations between wing length and other body size measures for females. Bill height correlated most strongly with wing length ($r^2 = 0.44$, $P < 0.0005$,

$n = 25$, power = 0.96). The regression equation (wing length = 91.851 + 3.701*bill height) was used to estimate wing length for breeding females in 1999/2000. Relative feather length, P9 length divided by wing length derived from this equation, was used to study moult progression.

Nestling mass (±1 g) and tarsus length (±1 mm) were measured every 4 days. Sometimes these measurements had to be estimated at the time of female departure from the nest. We calculated average daily change between the last measurement taken prior to female departure and the first measurement taken subsequent to female departure, and assumed uniform growth over this period. We used the ratio of mass to size (tarsus length for nestlings and bill length for females; g/mm) as a measure of body condition, hereafter called mass–size ratio. Mean nestling mass and mass–size ratio were calculated per nest and used instead of individual measures to avoid pseudoreplication (Hurlbert 1984). It may be inappropriate to compare mass–size ratios of nestlings of different ages (Jakob *et al.* 1996, Kotiaho 1999, Marshall 1999). Growth curves for nestling mass and tarsus length differ substantially, so that similar ratios of mass to length may fail to represent similar body condition at different stages of development. We therefore interpret these results over short-term intervals only.

Lastly, male provisioning prior to female departure from the nest was observed during one 3-h session less than 3 days prior to female departure ($n = 7$ nests). Observations were confined to cooler parts of the day, to avoid periods when feeding activity was suppressed. An observation hide was placed 10–30 m from the nest and binoculars used to record the type of prey delivered and its approximate size. Often prey size was confirmed by means of a pinhole camera (CCD pinhole with 3.5-mm lens aperture; two 3 IR-emitting diodes; Sony TRV110E video camera), placed inside the nestbox as part of another study. Three size classes were identified, relative to bill length, namely small (< 10% length), medium (10–25%) and large (> 25%). Males varied in their wariness to the presence of hides. To control for male wariness, we only calculated provisioning rates starting from the second visit to the nest. Weighted provisioning rate (weighted feeds per hour) for each session was calculated by weighting small items 1, medium items 3 and large items 5.

Data analyses were conducted using Statistica (StatSoft, Inc.) or performed by hand following Zar (1999). Appropriate tests were conducted after testing for normality by means of Kolmogorov–Smirnov tests ($P > 0.2$) and homoscedasticity by means of Levene tests ($P > 0.05$). Temporal change is illustrated with time series plots relative to the date of female departure from the nest.

RESULTS

Nestling development and food limitation

Nestling tarsus length at female departure from the nest did not correlate with nest depth for any of the nestlings, or for mean nestling tarsus length per nest ($r^2 = 0.05$, $P > 0.4$, $n = 15$; power > 0.95; Zar 1999) (P5). Pinhole camera observations inside the nestboxes showed that some nestlings were incapable of reaching food passed to them through the nest entrance slit, or of defecating through the entrance slit (P4). The floors of some nests, as well as the nestlings' plumage, beaks and legs, were covered in a layer of dried faeces.

Nestling mass grew logistically, levelling off more than 15 days after female departure (Fig. 1). There was neither an obvious slowing of nestling growth prior to female departure nor an increase in rate of growth subsequent to female departure (P2). Although variability in mean nestling mass did vary with time (Bartlett's test: $\chi^2 = 64.4$, $P < 0.001$, $n = 14$), there was no sign of a reduction in variability at or before female departure (Fig. 1). Nestling mass–size ratio approximated to a negative exponential function, showing no obvious changes in slope at the time of female departure (Fig. 2; P1). Again, variability in mean mass–size ratio did vary with time (Bartlett's test: $\chi^2 = 42.3$, $P < 0.001$, $n = 14$) but showed no reduction at or before female departure.

The duration of the female's stay in the nest was not dependent on either mean nestling mass at departure (linear regression: $F = 0.006$, $P < 0.95$, $n = 14$ nests) or mean nestling mass–size ratio at departure (linear regression: $F = 0.001$, $P < 0.975$, $n = 14$ nests; P1 & 2). It was also unrelated to her partner's ability to provide food (linear regression: $F = 2.040$, $P < 0.25$, $n = 7$; power of correlation = 0.78; P7). Furthermore, females with partners with low provisioning rates (fewer than three weighted feeds per hour; $n = 3$; mean = 55 days) did not stay significantly longer than those with high provisioning rates (more than seven weighted feeds per hour; $n = 2$; mean = 60 days) (Lord's range test (Langley 1968): $P > 0.05$, $n = 5$; P7). Lastly, the duration of the female's stay in the nest did not vary according

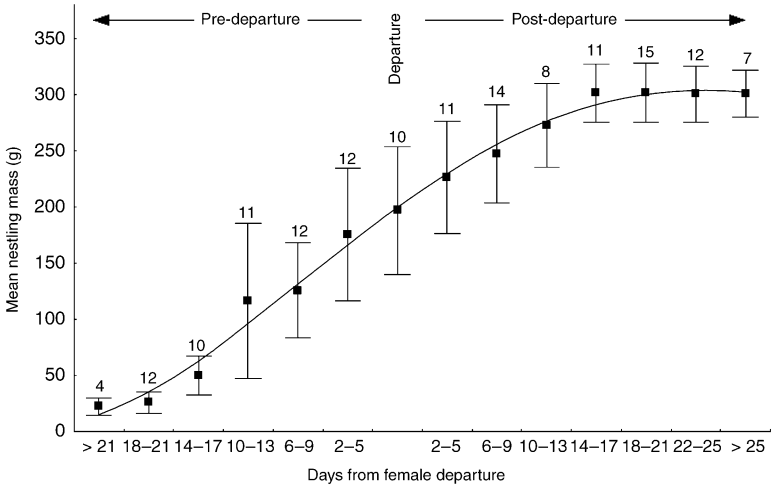

Figure 1. Change in mean (± sd) nestling mass per nest (g) relative to the time of female departure from the nest (*n* indicated above data points). A fourth-order polynomial curve is fitted to indicate the trend, with growth approximating a logistic curve.

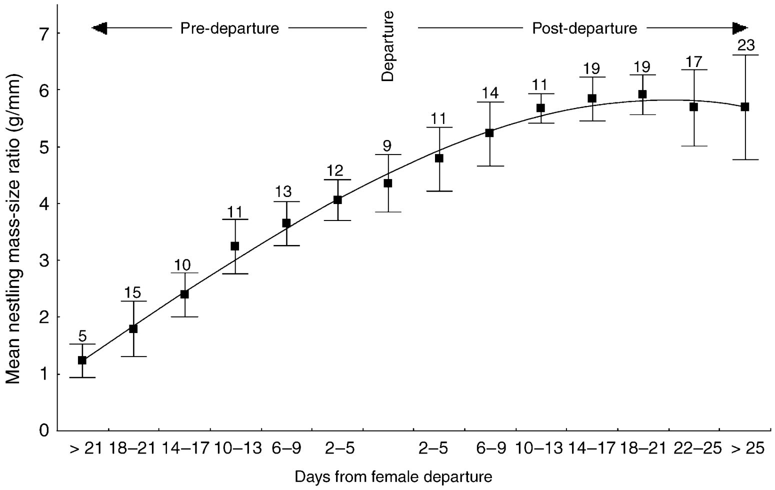

Figure 2. Change in mean (± sd) nestling condition per nest (mass/tarsus length; g/mm) relative to the time of female departure from the nest (*n* indicated above data points). A third-order polynomial curve is fitted to indicate the trend.

to her clutch size (Kruskal–Wallis ANOVA: $H = 7.204$, $P < 0.15$, $n = 54$, power of correlation = 0.52; P8).

Female condition and completion of moult

From a peak in mass and condition 24–27 days prior to female departure, when eggs started to hatch, mass and condition were lost to reach a minimum at female departure (Fig. 3). From *c.* 15 days prior to departure, the standard deviation in condition and mass between females decreased rapidly (Fig. 4). Immediately prior to departure females were more similar to one another as regards condition (Bartlett's test: $\chi^2 = 18.5$, $P < 0.05$, $n = 11$) and mass than at any other stage during their stay in the nest (P3).

Primary feather growth approximated to a logistic curve, with feather length showing indications of reaching an asymptote at female departure (Fig. 5; P6). Variability in primary feather length between females increased to a maximum 15–19 days prior to departure (Fig. 6). Over the last 2 weeks, variability between females decreased rapidly, reaching a new stable minimum at departure. Variability in moult progression differed at different stages prior to departure (Bartlett's test: $\chi^2 = 156.6$, $P < 0.0001$,

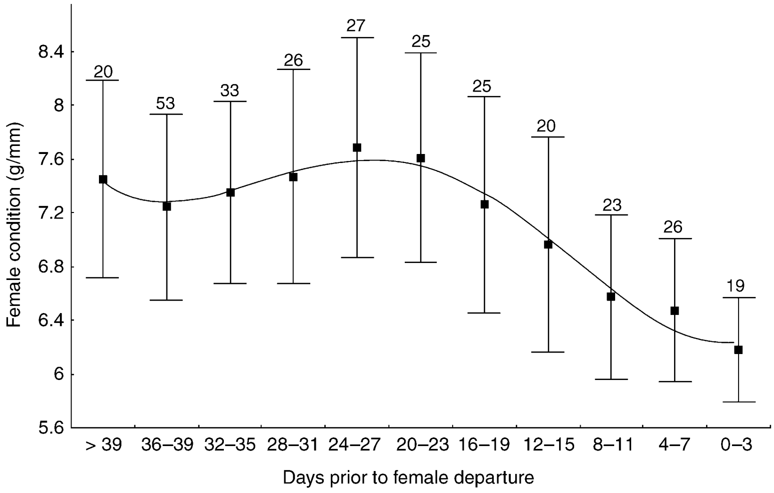

Figure 3. Change in female condition (g/mm) relative to the time of female departure from the nest (mean ± sd; *n* indicated above data points). A fourth-order polynomial curve is fitted to indicate the trend.

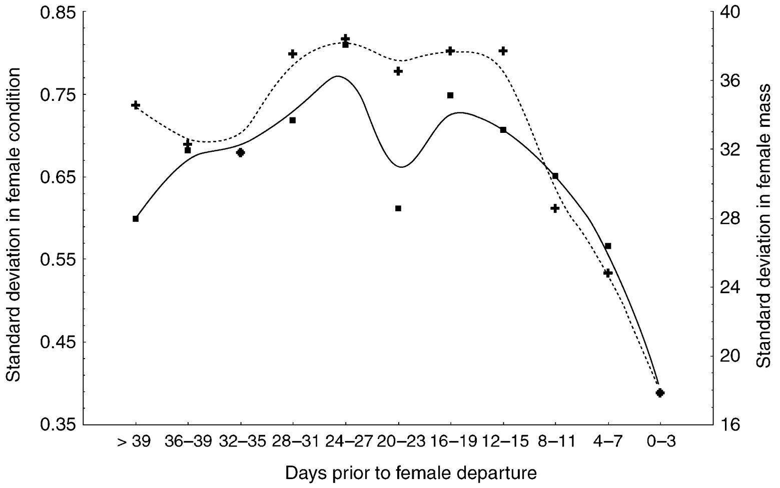

Figure 4. Change in the standard deviation in female condition (left axis; crosses) and female mass (right axis; squares) relative to the time of female departure from the nest (*n* as for Fig. 3). Least-squares functions are fitted to indicate the trend for condition (dotted line) and mass (solid line).

n = 9), with females leaving in near identical states of moult (P6).

DISCUSSION

In this study no predictions are met that support the hypothesis that the timing of the female Monteiro's Hornbill's departure from the nest is determined by factors associated with the condition of nestlings. As expected, females appear not to base the decision on when to depart in order ultimately to maximize their current reproductive output. Nestling development, e.g. tarsus length, has no detectable influence, because nestlings do not need to reach the nest entrance to obtain food (P4 and P5). Poor sanitation may have subtle effects on nestling survival, owing to increased disease or parasite load, but natural nest cavities used by Monteiro's Hornbill are usually shallower than those of nestboxes used in this study, with even small nestlings being able to defecate out of the nest (C. Boix-Hinzen pers. obs.).

There is also no evidence that female departure was determined by nestling growth or condition (P1 and P2). It is possible, however, that females may

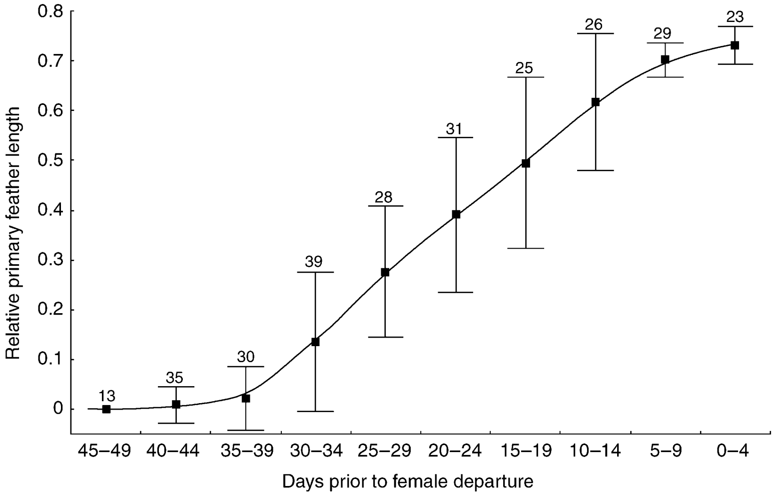

Figure 5. Change in relative length of primary feather 9 (feather length/wing length) relative to the time of female departure from the nest (mean ± sd; *n* indicated above data points). A least-squares function is fitted to indicate the trend (Statsoft, Inc.).

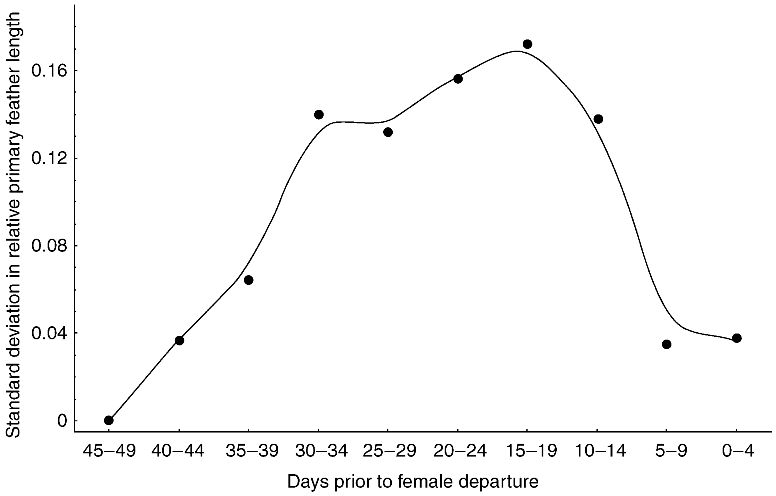

Figure 6. Change in standard deviation of relative length of primary feather 9 with time to female departure from the nest (*n* as for Fig. 5). A least-squares function is fitted to indicate the trend (Statsoft, Inc.).

depart in response to subtle signals, such as hunger, which allow them to time their departure prior to food shortage, thereby having an effect on nestling growth and mass–size ratio (P7 and P8). In addition, high seasonal rainfall during this study created conditions of food abundance – large quantities of uneaten food remained in some nests and male provisioning was far higher than reported by Kemp and Kemp (1972) – potentially masking patterns that may become apparent under conditions of food stress. Under conditions of food stress, younger nestlings are out-competed by older nestlings, causing them to lose mass relative to their size rapidly, and which may result in starvation (C. Boix-Hinzen unpubl. data). This should result in an increase in variability in mass and condition between nestlings, a pattern that did not emerge in our data.

Both predictions in support of the hypothesis that female departure is determined by factors associated with her own state, and thus with factors that ensure female survival and future reproduction, were met (P3 and P6). Not only were the mass and condition of females at their lowest when the female left the nest, but prior to departure variability in female condition and mass decreased dramatically (P3). This is indicative of strong stabilizing selection, in which variability in factors determining the timing of departure, e.g. female condition, narrows around the optimal condition.

Although losses in female mass and condition suggest that females may have been under food stress, the amount of uneaten food in some nests suggests otherwise. Females certainly had the option of feeding more. Slimming prior to departure is unlikely to have costs to females, at least until a threshold is reached. It is also unlikely to be related to the fact that females must be small enough to pass back through the entrance of the nest, as they are much heavier when they enter the nest than when they depart.

Although the timing of female moulting seems to have evolved to maximize energy availability to nestlings (Klaassen *et al.* 2002), its timing has no clear cost to females. According to Klaassen *et al.* (2002), the timing of the female's departure from the nest is carefully scheduled to reduce the male's workload, despite her departure occurring some time (*c.* 5–11 days; Kemp 1995) before the peak energy demands of nestlings occur. Furthermore, this hypothesis assumes that nestling growth ultimately drives provisioning, and not vice versa.

Female feather re-growth is also strongly associated with the timing of her departure from the nest (P6). Not only did primary feathers virtually stop growth by the time the female departed, but all females left the nest in near identical condition. This again suggests a strong stabilizing selection around optimal conditions of feather re-growth. Although negative effects of premature departure are not known, these data suggest that optimal conditions are important and should be adaptive and have consequences for survival.

The Monteiro's Hornbill is long-lived and inhabits highly variable and unpredictable environments (Kemp 1995). The hypothesis that life-history evolution in the Monteiro's Hornbill should favour adult survival, a measure of future reproductive success, in trade-offs with current reproductive output, is well supported by this study. Basing the timing of female departure on her own condition and moult completion is likely to maximize her own survival. This promotes iteroparity and future reproductive opportunity, a key strategy in maximizing lifetime reproductive success, and ultimately in individual fitness.

The timing of female emergence apparently has a strong phylogenetic component among hornbill species, and is unrelated to size (Kemp 1995). Other genera of hornbills, e.g. *Bycanister* and *Aceros*, seem to delay their departure from the nest to some time after moulting has been completed. This later departure, if adaptive, is likely to be due to the female having some role in the nest, such as food processing and distribution or nest sanitation. Alternatively, females may be 'exploiting' the male's provisioning by remaining in the nest as long as the male brings food to the nestlings, and may thus be dependent on male provisioning and/or on nestling growth and size-dependent mass. The timing of female departure from the nest in other *Tockus* species may well be related more strongly to other factors. We suspect that the Southern Yellow-billed Hornbill *T. flavirostris*, which usually occurs in more mesic woodlands than Monteiro's Hornbill, invests more energy in any breeding season than does Monteiro's Hornbill. Even in seasons of poor rainfall they manage to produce average-sized clutches (C. Boix-Hinzen unpubl. data). In species such as *T. flavirostris*, where investment in current reproduction is high, there may be a lower threshold level of female condition that would drive females to leave the nest, making it more likely that other factors such as nestling condition may drive female departure. Variability among the hornbills with regards to relative departure time and various life-history traits has potential for an interesting comparative study.

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